Research Article

Mangrove-associated Pacific oysters (*Magallana gigas*) influence estuarine biodiversity

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Abstract

Estuarine ecosystems are often characterised by endemic foundation organisms which facilitate ecosystem interactions and processes established over millennia. Introduction of non-native foundation species can significantly alter ecological communities and functions. Here, we assessed the effects of introduced, reef-forming Pacific oyster *Magallana gigas*, within a temperate Australian mangrove-dominated estuary. Specifically, we investigated whether mangrove-attached *M. gigas* oyster reefs influenced intertidal fish and invertebrate communities, and fish foraging behaviour. We measured and contrasted the benthic structure and faunal communities of fringing bare sediment, *Avicennia marina* mangrove and Pacific oyster *M. gigas* reef habitats using a combination of quadrats, fyke nets and remote unbaited video (RUV) surveys. Pacific oyster reefs showed no impacts on pneumatophore density or morphology, but were positively associated with higher seedling densities. Furthermore, invertebrate and fish community metrics (e.g. richness, biomass, length) were typically higher in *M. gigas* reefs compared to the other habitats. However, several mobile, non-native species were predominantly detected in *M. gigas* reefs, including exotic gobies and European shore crabs *Carcinus maenas*, a declared marine pest. Overall, we found that *M. gigas* reefs in fringing mangrove forests were associated with biodiverse faunal communities, including fisheries-targeted species, but also facilitated other non-native species. These outcomes highlight some of the ecological pros and cons of non-native oyster reefs and the complexity of managing estuaries globally where Pacific oysters increasingly co-occur with endemic habitat-forming species.

Key words: Biogenic, facilitation, habitat-formers, invasive species, mangroves, nekton, shellfish, temperate

Introduction

In estuarine systems, habitat-forming, foundation species including mangroves, seagrass, oysters and coral, influence community composition and ecosystem functioning (Dayton 1972; Angelini et al. 2011). Habitat-formers directly modify the physical structure and biogeochemical processes and indirectly influence the environment from the activities of other organisms they facilitate. Subsequently, habitat-formers support valuable ecological services including fish production, nutrient cycling and coastal protection (Barbier et al. 2011; zu Ermgassen et al. 2021). For example, mangroves protect coastal infrastructure and stabilise otherwise bare coastal margins (Marois and Mitsch 2015). Globally, mangrove forests

also store an estimated 5.85 Pg of carbon (Alongi 2020). Similarly, oyster reefs remove excess nitrogen via biofiltration (Ray and Fulweiler 2021) and are used as nursery habitats by fisheries-targeted nekton (Gilby et al. 2018; zu Ermgassen et al. 2021). Positive ecological functions can be further enhanced by multiple, co-existing habitat-formers, which interact to increase structural and functional heterogeneity, leading to facilitation cascades that enhance niche availability and species biodiversity (Thomsen et al. 2022). As an example of a facilitation cascade, intertidal bivalve recruitment and survival may be enhanced by the shading of saltmarsh plants, which in turn, benefit from greater sediment stabilisation and en-richment provided by the bivalves (Gagnon et al. 2020), with their co-occurrence facilitating enhanced invertebrate biodiversity (Angelini et al. 2015). Conversely, when a habitat-former is introduced outside its native range, it can have mixed and context-specific outcomes, including "negative" impacts, such as declines in endemic biodiversity, ecosystem functions or services; or "positive" impacts, the opposite (Guy-Haim et al. 2018; Rilov et al. 2024).

Invasions by non-native species can significantly modify ecological communi-ties and functions, often decreasing species abundance and diversity via negative interactions including competition, predation and altering environmental con-ditions (Gallardo et al. 2016). Non-native habitat-formers, specifically, can have ecosystem-scale impacts via habitat alteration (Rilov et al. 2024). For instance, the non-native seagrass *Halophilia stipulacea* has displaced native seagrasses in the Caribbean, altering invertebrate communities and limiting nutrient availability (Muthukrishnan et al. 2020). Conversely, non-native habitat-formers may enhance biodiversity, including native (Rodriguez 2006) and other non-native species (i.e. 'secondary invasions', O'Loughlin and Green (2017)). For example, in northern Europe, Pacific oyster *Magallana gigas* (formerly *Crassostrea*) reefs support valuable ecosystem services including nutrient cycling (Zwerschke et al. 2019), shoreline protection (De Vriend et al. 2014) and enhanced shorebird foraging opportunities (Herbert et al. 2018). Zwerschke et al. (2019) proposed that non-native *M. gigas* reefs may restore the ecological functions of almost extinct native oysters *Ostrea edulis* reefs, with McAfee and Connell (2021) suggesting that the global spread of this invader potentially compensates for the worldwide loss of > 85% of endemic oyster reefs (Beck et al. 2011).

Pacific oysters, endemic to the north-west Pacific, have been introduced delib-erately for aquaculture and unintentionally through shipping and are now globally distributed on every continent, except Antarctica (McAfee and Connell 2021). They are favoured in aquaculture because of their fast growth rate, high reproduc-tive output and relatively low disease mortality (Troost 2010; Stechele et al. 2022). These traits have also supported invasive *M. gigas* populations establishing in 36 countries, as reviewed by Martínez-García et al. (2022). In the future, *M. gigas* may also spread to dominate most temperate coastlines (McAfee and Connell 2021), with projected climate change conditions favourable to their poleward expansion (King et al. 2021). The proliferation of invasive *M. gigas* populations has created a dilemma for coastal management between encouraging non-native oyster produc-tion and restorative aquaculture (van der Schatte Olivier et al. 2020; Theuerkauf et al. 2022), versus mitigating the potential socioecological impacts of non-native oyster reefs (Forrest et al. 2009; Herbert et al. 2016).

As summarised in recent literature reviews (e.g. McAfee and Connell (2021); Hansen et al. (2023)), invasions by *M. gigas* are associated with mixed ecological

outcomes for endemic communities, which are context- and scale-dependent. For example, Andriana et al. (2020) showed with manipulative plots that Pacific oysters outcompete native blue mussels (*Mytilus edulis*) and displace native habitat-forming seaweeds in the Walden Sea. Work in this same region has also shown that Pacific oysters can influence parasite infections in *M. edulis*, functioning as vectors for disease transmission (Goedknegt et al. 2019). Furthermore, Bazterrica et al. (2022) investigated Pacific oyster reef impacts in Argentinean soft-sediment habitats, identifying that these oyster reefs supported high densities of exotic and cryptogenic invertebrates that were absent from uninvaded cordgrass and bare sediment areas. Conversely, small-scale studies assessing *M. gigas* impacts on invertebrate communities have found comparable assemblages to endemic bivalve ecosystems in northern Europe (Zwerschke et al. 2019) and Australia (Wilkie et al. 2012) suggesting habitat redundancy. Additionally, manipulative subtidal trials in Sweden assessed the habitat value of *M. gigas* versus *M. edulis* shells using drop samplers and found higher abundances and biomass of epibenthic fauna associated with the Pacific oysters (Norling et al. 2015). These examples indicate that the net impacts of non-native *M. gigas* are complex and mediated by a combination of environmental conditions, habitat structural characteristics and interactions with local biological communities.

Pacific oysters were introduced to temperate Australia in the 1940s for oyster aquaculture and they have since established invasive populations, primarily managed as an aquaculture biosecurity risk (Gillies et al. 2018). In Australian estuaries, *M. gigas* may form oyster reefs on consolidated structures (Gillies et al. 2018) and function as secondary habitat-formers attached to grey mangroves *Avicennia marina*, a primary habitat-former (Bishop et al. 2010; Wilkie et al. 2012). This region formerly supported extensive native oyster reefs till the mid-20th century, with estimated losses of > 99% of flat oyster *Ostrea angasi* reefs and > 90% of Sydney rock oyster *Saccostrea glomerata* reefs (Gillies et al. 2020). Subsequently, non-native *M. gigas* reefs may provide an unintended offset to the loss of native oyster reefs in temperate Australia, contrary to contemporary models of habitat decline (Davis et al. 2011; McAfee and Connell 2021).

Despite the growing distribution of non-native oyster reefs worldwide, previous research on their ecological impacts has primarily focused on their impacts to sedimentary communities particularly in Europe (Padilla 2010). Furthermore, few studies have investigated how *M. gigas* reefs influence fish communities (Martin et al. 2024) or their ecological impacts in mangrove forests (Bishop et al. 2010; Gagnon et al. 2020). To address these knowledge gaps, this study investigated fish and invertebrate community composition and habitat occurrence, with comparisons across *M. gigas* oyster reefs and uninvaded bare sediment and *A. marina* mangrove habitats, within a temperate Australian estuary. Specifically, it tested the hypotheses that: (1) *M. gigas* oyster reefs were associated with lower mangrove pneumatophore densities and sizes compared to uninvaded mangroves; (2) greater sediment organic matter percentages from biodeposition, as compared to other habitats; (3) that oyster reefs support greater invertebrate and fish species richness, relative total abundances, combined invertebrate biomass and fish foraging (total bites), compared to other fringing estuarine habitats; and (4) support distinct invertebrate and fish communities to other habitats. This study provides critical insights for evaluating the ecological role of non-native oysters and understanding their interactions with estuarine mangroves, invertebrates and fish communities.

Methods

Site description

The Port River-Barker Inlet Estuary is the largest estuary in Gulf St. Vincent, Australia (34°47'S, 138°31'E; Fig. 1) and the main maritime port for South Australia's capital city of Adelaide since 1837. The Estuary is highly modified from pre-European conditions, with significant declines in coastal vegetation and native shellfish ecosystems due to urbanisation, pollution and channel modifications (Edyvane 1999). Non-native marine species, such as Pacific oysters (*Magallana gigas*), have also become established within the Estuary, with *M. gigas* first detected from intentional, but unauthorised introductions of hatchery stock in 2009 (Wiltshire et al. 2010). Pacific oysters presently occur throughout the Estuary, primarily attached to artificial structures (e.g. rock levees, pylons), grey mangroves (*Avicennia marina*) and bivalve shells.

This study was situated within the Port River-Barker Inlet Estuary along the western shoreline of Torrens Island, which fringes the main Port River channel (Fig. 1). We sampled three habitat types along a two-kilometre low intertidal fringing zone:
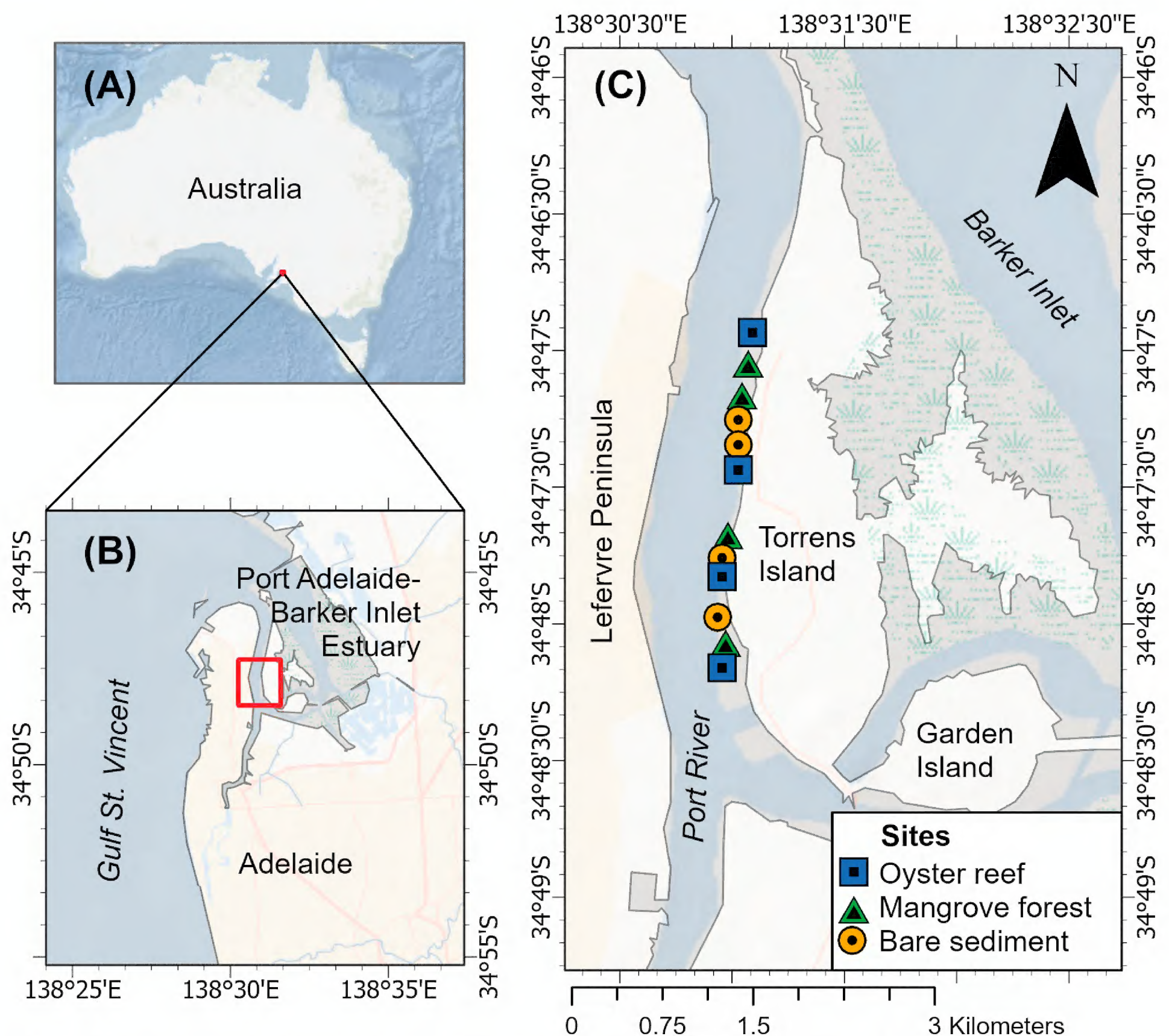

Figure 1. Location of **A** Adelaide in South Australia **B** the Port River-Barker Inlet Estuary and **C** sites of the three surveyed habitat types.

grey mangrove (*Avicennia marina*) forests, used as a natural structured control site, bare sediment and nested *Magallana-Avicennia* oyster beds (hereafter 'oyster reefs'). Four replicate sites for each habitat (bare sediment, mangroves, oyster reef; Fig. 2) were haphazardly selected (n = 12; Fig. 1). All sites were situated in the mid-intertidal zone above the lowest astronomical tide (LAT) line and were submerged during high tide. Sites were comprised of continuous habitat that extended for ≥ 30 m stretches and separated from other sites by ≥ 30 m. Oyster reefs were comprised of pneumatophore-attached *M. gigas* shell clumps (alive and deceased oysters) which occurred as 50–60 m length patches, extending 5–10 m seawards of fringing mangroves. Reef shell material had a minimum vertical relief of ≥ 50 mm above the surrounding sediment, with typical alive adult (> 25 mm length; Markert (2020)) oyster densities of ≥ 200 ind. m^{-2} (Herbert et al. 2016). Mangrove sites consisted of 50–100 m stretches of fringing old-growth and immature *A. marina* with few or no alive, adult oysters (i.e. < 25 ind. m^{-2}). Bare sediment sites ranged from 30–75 m in length and were characterised by continuous, low-relief habitat of mud/sand and microalgae mats. All site surveys occurred during late February and March 2023.

Quadrat surveys

We characterised site-specific structures during low tide using eight (0.5 × 0.5 m) haphazardly placed photographic quadrats (n = 96; Fig. 2). Photographs were assessed in ImageJ (WS 2011) to estimate benthic cover composition (%) and densities of mangrove seedlings (i.e. < 30 cm height) and pneumatophores. Benthic cover categories were bare sediment, cockle (*Katelysia* spp.) shell, mangrove roots and seedlings and oyster (*Magallana gigas*) shell. Four quadrats per site (n = 48) were excavated to quantify additional structural components and associated macrofauna. Firstly, the aboveground height and basal diameter of up to six haphazardly selected pneumatophores were measured using vernier callipers (to 0.1 mm). Next, we removed all shell material, mobile macrofauna (invertebrates and fish) and the top five centimetres of sediment for processing, including partially buried oyster material (e.g. Grabowski et al. (2005)). Loose material was sieved *in situ* through a 1-millimetre sieve before being bagged, transported to the laboratory and frozen (-20 °C).
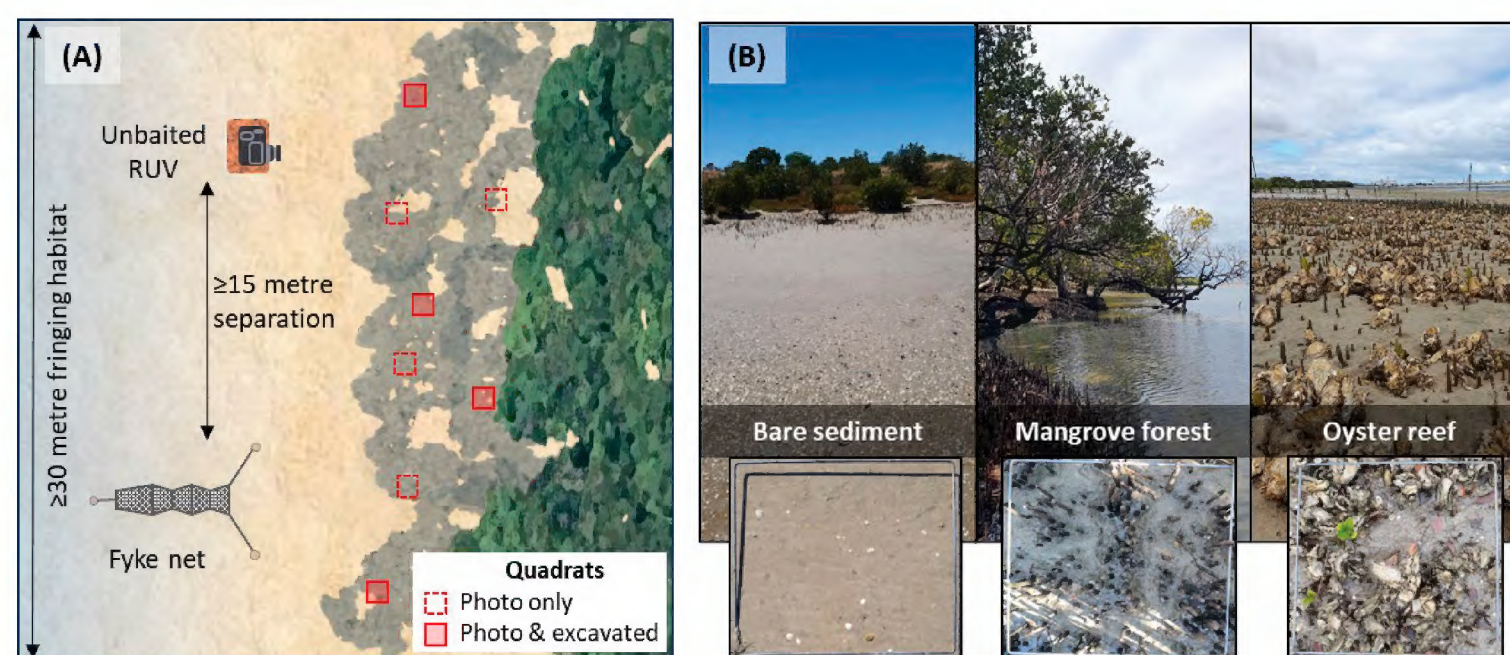

Figure 2. Representative images of **A** simplified survey design used to assess estuarine assemblages at each site, with an unbaited remote underwater video (RUV) system and a fyke net (deployed at high tide) and haphazardly placed quadrats (surveyed at low tide) **B** examples of the surveyed habitats and associated photo-quadrats for bare sediment, mangrove (*Avicennia marina*) forest and mangrove-attached Pacific oyster (*Magallana gigas*) reefs.

In the laboratory, we defrosted, rinsed and sorted the retained material from the excavated quadrats. Firstly, we enumerated oysters and classified them as either alive juveniles (< 2 mm), alive adults (> 25 mm), dead cups (open shell without the top valve) or dead boxes (open shell with two articulated valves). Up to 20 randomly selected alive juvenile and adult oysters per quadrat were measured for shell heights (i.e. longest hinge-lip distance, to 0.1 mm). Additionally, we measured the total biomass oyster and cockle shell material, respectively, using an electronic scale (0.1 g). Total oyster biomass included both the shell and wet meat weights as dead and alive oysters occurred as clumped material, whereas cockle shells consisted of disarticulated and fragmented material. We inspected all shell material for macrofauna, which we enumerated, weighed (wet weight, 0.01 g) and identified to the lowest practical taxonomic level using field guides (e.g. Gowlett-Holmes (2008)).

Nekton surveys

We surveyed nektonic fish (teleosts and elasmobranchs), decapods and cephalopods using a combination of unbaited remote underwater video (RUV) stations and extractive fyke nets (Fig. 2; Martin et al. 2024). We concurrently deployed pairs of RUV and fyke nets from shore across the twelve sample sites over two subsequent days of daylight high tides, with sampling repeated across three sample periods on a fortnightly basis (n = 36). We positioned all survey gear ≥ 15 metres apart during daytime (8:00 to 16:00 h) high tides, in ≈ 1.5 metre depths, for a continuous 90-minutes soak-time.

Each RUV consisted of a single weight-attached GoPro Hero 7/8 camera positioned 20 cm above the benthos. Stations were unbaited to avoid bait-biases influencing habitat use (Bradley et al. 2016). We annotated video records in Event-Measure (SeaGIS 2023) with all nekton counted and identified to the lowest taxonomic level (Gomon et al. 2008). Due to differences in recording duration across RUV surveys, we only annotated the first 60-minutes of each video, commencing 1 minute after deployment to allow disturbed sediment to settle. We calculated the maximum number of individuals of the same species present within a single frame from each video (MaxN), which is a commonly used, conservative abundance metric (Whitmarsh et al. 2016). We also recorded fish foraging behaviour by counting the number of bite interactions observed between fish and the benthos.

We deployed unbaited fyke nets (0.4 m ø opening, fyke mesh size 1.2 mm²; with 2 m x 1.2 m wings; 4 m total length), with the net opening facing the shoreline to sample fish on the ebbing tide (Fig. 2). We removed captured organisms from the net and placed them on to a scaled-grid where we photographed, enumerated, identified them to species level, then released them (except voucher specimens). From each fyke-net deployment, we determined the length measurement of ≤ 20 individuals from voucher specimens and photographs in ImageJ, recorded as either total length (fish), carapace length (decapods) or mantle length (cephalopods) (to 1.0 mm). For any unidentifiable fishes, we euthanised voucher specimens using an overdose of Aqui-S and transported them to the laboratory for identification and measurement.

Abiotic variables

We recorded water temperature (°C) using a multiparameter probe (Polaris C, OxyGuard) and salinity (PPT) using a handheld refractometer prior to each RUV and fyke-net deployment. We estimated distances to estuary mouth from each site

using GoogleEarth by measuring the contour along the river edge, as well as distances to the channel edge, representing subtidal refugia (to 1 m). Three replicate sediment samples (≈ 50 g) were collected from each site, transported to the laboratory and immediately frozen. We dried approximately 10 g of defrosted sediment from each sample at 60 °C for at least 4 days, prior to incineration at 450 °C for 4 hours. We then calculated the percentage of sediment organic matter as the difference in weight between pre-combusted and post-combusted sediment.

Statistical analyses

We carried out all statistical analysis in Rstudio (Version 4.3.1; R Core Team 2024). We used non-parametric Kruskal-Wallis chi-squared tests to assess differences in fine-scale habitat components including benthic cover percentages; densities of mangrove structures and shells, shell biomass and sediment organic matter (%). When significant ($p < 0.05$), we used Dunn's post-hoc tests for pairwise comparisons between sites. Mann-Whitney U-tests were used to assess differences in pneumatophore height and diameter between the mangrove and oyster reef sites.

To evaluate the effects of habitat and environmental variables on univariate community metrics (richness, density, biomass) from the quadrats, we first used the Pearson's correlation coefficient to remove collinear predictors ($|r| > 0.7$; Suppl. material 1: fig. S1A). The refined model of environmental predictors included estuary mouth distance, pneumatophore densities, seedling densities and cover (%), cockle shell biomass, oyster shell biomass and sediment organic matter (%). We used Generalised Linear Models (GLMs) to evaluate differences in the univariate invertebrate variables (e.g. species richness, biomass and densities) using the refined model and habitat treatment categories. We assessed species richness using a Poisson distribution, while biomass and density were modelled using negative binomial distributions to meet assumptions of normality and heteroscedasticity. Any significant habitat differences from Analysis of VAriance (ANOVA) results were further assessed using Tukey pairwise comparisons. Modelling was performed using the *PMCMRplus* (v. 1.9.10 Pohlert 2018) and *MASS* packages (v. 7.3-60 Ripley 2011).

Habitat differences in the multivariate community composition from the excavated quadrats was assessed with the *vegan* package (v. 2.6-4, Oksanen et al. 2013) using the PERmutational Multivariate ANalysis of VAriance (PERMANOVA) across Habitats (3 levels, fixed: oyster reef, mangroves and bare sediment) with estuary mouth distance as a covariate. Prior to analysis, we assessed and visualised potential skewness using a series of transformations and shade plots, to achieve a normal distribution. We used fourth-root transformation to reduce the effects of overly abundant invertebrates, before calculating Bray-Curtis dissimilarly matrices. Subsequent post-hoc pairwise PERMANOVA tests assess significant pairwise habitat differences. We then conducted Dufrene-Legendre indicator species analysis using *Labdsv* package (v. 2.1-0, Roberts and Roberts 2016) to identify the species that most contributed to differences between habitat types. We then used a distance-based ReDundancy Analysis (dbRDA) to ordinate the transformed community data and identify relationships with the environmental variables. Using the 'envit' function of the *vegan* package, vectors from the environmental variables were tested for significant ($p < 0.05$) correlation to the ordination axes (9999 permutations) and fitted to the dbRDA plot as overlaid vectors. We also overlaid the Pearson correlations between the indicator species abundances and community data to visualise the strength and direction of associations.

Assessments of nekton communities followed similar steps to those used to assess the assemblages from the excavated quadrats. Firstly, we averaged habitat quadrat variables (e.g. habitat cover %, shell densities) to obtain site-level estimates to use as predictors. Collinear environmental predictors were then removed, based on the Pearson's correlation coefficient ($|r| > 0.7$; Suppl. material 1: fig. S1B). This refined the predictors to estuary mouth distance, percentage cover of *A. marina* seedlings and pneumatophores, cockle shell biomass, oyster shell biomass and water quality parameters (salinity, dissolved oxygen, temperature). Subsequent General Linear Modelling assessed predictors for total abundances and species richness from each survey methods and fish bite counts from the RUV surveys. The GLMs used the refined model of environmental predictors, as well as the factors of Habitat (3 levels) and Sampling Period (3 levels). We assessed species richness using Poisson distributions and used negative binomial distributions for the abundance and count data, based on model requirements.

We investigated potential habitat differences in multivariate nekton assemblages using PERMANOVA tests of Bray-Curtis dissimilarly measures on the square-root transformed data obtained from the RUV and fyke-net surveys, respectively. We added a dummy value to the fyke-net matrices to allow the inclusion of samples containing no nekton. Each PERMANOVA included Habitat (fixed factor; three levels), Sample Period (fixed factor; three levels) and estuary mouth distance as a covariate, with post-hoc pairwise PERMANOVA tests used to examine any habitat differences. We then conducted Dufrene-Legendre indicator species analysis and identified any significantly correlated environmental predicators using 'envfit'. The results were then visualised as distance-based ReDundancy Analysis (dbRDA) plots. Finally, we assessed the size-frequency distribution of all species measured from the fyke nets using Kruskal-Wallis chi-squared tests, with Dunn's post-hoc tests used to assess pairwise differences in nekton species length by habitat type.

Results

Environmental and structural characteristics

Quadrat sampling revealed fine-scale variability within habitats and broader structural differences across habitat types (Table 1, Fig. 2). All benthic habitat cover percentage categories significantly differed across habitats (Table 1; Dunn's Post-hoc: $p \leq 0.004$). Pairwise comparisons supported the proportional dominance of bare sediment cover (%) in bare sediment habitats, as compared to mangrove and oyster reef habitats. Both of these structured habitats had similar percentage cover proportions of cockle shells ($p = 0.33$) and pneumatophores ($p = 0.43$; Table 1). Mangrove and oyster reef habitats also had similar pneumatophore densities ($p = 0.78$) and contained an average of 254 ± 20 pneumatophores m^{-2}.

Oyster reefs had significantly higher proportional cover of oyster (*Magallana gigas*) shells compared to the other habitats, with an average cover of 31.21 ± 2.87 percent (Table 1). This is consistent with the high densities of adult alive oysters (average $\pm$ SE: 254 ± 32 ind.m^{-2}) and oyster shell biomass (13.15 ± 1.52 kg.m^{-2}). Cockle (*Katelysia* spp.) shell biomass was also higher in oyster reefs ($p \leq 0.001$), but similar amongst the other habitats ($p = 0.19$). The proportional cover and densities of mangrove (*Avicennia marina*) seedlings were also higher in oyster reefs ($p \leq 0.016$ and $p \leq 0.04$, respectively), compared to other habitats, with an average of $\approx 7 \pm 1$ seedlings ind.m^{-2}.

Table 1. Average ± standard error (SE) and range (min–max) of micro-habitat characteristics obtained from photo-quadrats (n = 96), excavated quadrats (n = 48) and sediment cores (n = 36). This includes measurements associated with the biogenic structures of grey mangroves (*Avicennia marina*), Pacific oyster (*Magallana gigas*) and cockle shells (*Katelysia* spp.). Post-hoc tests denote significant results of Kruskal-Wallis tests and pairwise Dunn's post-hoc comparisons between habitat types (*p* ≤ 0.05). Abbreviations: S = bare sediment, M = mangrove forests and O = oyster reefs.

Habitat characteristics	Bare sediment		Mangroves		Oyster reef		Post-hoc tests
	$\bar{x}$ ± SE	Range	$\bar{x}$ ± SE	Range	$\bar{x}$ ± SE	Range	
Habitat cover & mangrove structure densities from photo-quadrats (N = 96)							
Oyster shell %	0.07 ± 0.07	0–2.38	0.63 ± 0.28	0–6.84	31.21 ± 2.87	9.97–76.93	S < M < O
Bare sediment %	99.43 ± 0.20	93.96–100	88.47 ± 1.58	58.43–97.97	60.82 ± 2.84	17.45–81.55	S > M > O
Cockle shell %	0.48 ± 0.19	0–6.04	2.81 ± 1.25	0–38.15	1.51 ± 0.36	0–8.06	S < (M = O)
Mangrove roots %	-	-	7.39 ± 1.08	1.76–25.66	5.59 ± 0.66	1.18–15.51	S < (M = O)
Seedling %	0.02 ± 0.02	0–0.56	0.69 ± 0.24	0–5.11	0.87 ± 0.20	0–4.01	S < M < O
Pneumatophore roots.m^{-2}	-	-	250 ± 28	28–644	258 ± 27	60–624	S < (M = O)
Seedlings ind.m^{-2}	0.1 ± 0.1	0–4	3.1 ± 0.7	0–12	6.6 ± 1.1	0–24	S < M < O
Shell densities & weight from excavated quadrats (N = 48)							
Dead oyster ind.m^{-2}	-	-	0.50 ± 0.50	0–8	169 ± 27	36–468	(S = M) < O
Alive oyster spat ind.m^{-2}	-	-	0.50 ± 0.50	0–8	190 ± 60	0–812	(S = M) < O
Alive adult oyster ind.m^{-2}	-	-	2.25 ± 1.09	0–12	254 ± 32	88–532	(S = M) < O
Cockle shells g.m^{-2}	173 ± 66	0–948	392 ± 241	1–3880	594 ± 103	56–1,704	(S = M) < O
Oyster material g.m^{-2}	-	-	73 ± 40	0–536	13146 ± 1517	5,228–24,176	(S = M) < O
Sediment composition (N = 36)							
soil organic matter %	0.97 ± 0.12	0.53–1.75	2.17 ± 0.69	0.34–8.75	1.47 ± 0.28	0.53–1.75	S = M = O

The percentage of sediment organic matter was similar across habitats (Kruskal-Wallis: χ^2 = 3.297, *p* = 0.192), comprising 1.53 ± 0.26 percent on average, overall (Table 1). Measured water temperature and salinity across habitats ranged between 16.9 and 23.2 °C and 35 and 44 ppt, respectively.

Between the mangrove and oyster reef habitat treatments, no differences were detected in pneumatophore diameters (W = 4804, *p* = 0.359) or aboveground heights (W = 4074, *p* = 0.306), which had average (± SE) measurements across sites of 9.9 ± 0.2 mm and 89.4 ± 2.9 mm, respectively (Suppl. material 1, figure S2). We also measured 335 adult and 237 juvenile oysters, which indicated that most individuals were either spat (≤ 5 mm) or adults between 25 and 85 mm, to maximum length of 121 mm (Suppl. material 1: fig. S3A). Of the 2,469 oyster shells counted, 27% were dead 'cups' and 'boxes', with the remaining 73% split between alive adults (42%) and juveniles (31%, Suppl. material 1: fig. S3B).

Excavated quadrat assemblages

We collected 11,500 macrofaunal organisms (excluding oysters) belonging to 64 species and 12 taxonomic classes (Suppl. material 1: table S1). All species were invertebrates, except oyster blennies (*Omobranchus anolius*) (hereafter collectively termed 'invertebrates'). Oyster reefs were associated with 92% of invertebrate species, of which 21 species were exclusively found in this habitat, as compared to mangroves (3 species) or bare sediment (2 species). Most invertebrate abundance was comprised of minute air-breathing snails *Salinator fragilis* and *Hydrococcus brazieri* (33%) and clams *Lasaea australis* and *Scintillua solida* (18%). Ragworms (*Polychaeta* spp.), *S. fragilis* and *S. solida* were the most ubiquitous species, found in > 88% of quadrats. In contrast, the intertidal snails *Austrocochlea constricta* and

Bembicium auratum contributed the greatest combined biomass, representing 31% of total macrofauna weight. Quadrat surveys also detected 28 individuals invertebrates that are cryptogenic and/or non-native species, which were European shore crabs (*Carcinus maenas*), mud creepers (*Batrillaria australis*), Hercules club whelks (*Pyrazus ebenius*) and Sydney cockles (*Anadara trapezia*), 97% of these organisms being surveyed from the oyster reef habitats (Suppl. material 1: table S1).

Excavated quadrats from the oyster reefs typically supported at least two times greater species richness (average ± SE: 23.9 ± 1.2 species), 1.8 times greater densities (1,534 ± 191 individuals.m^{-2}) and 7.6 times more invertebrates biomass (426 ± 84 grams.m^{-2}) than the other two habitats (Fig. 3). ANOVA tests indicated significant differences in the invertebrate richness, density and biomass amongst habitats ($p \leq 0.001$; Suppl. material 1: table S2A); however, post-hoc Tukey's tests indicate these were not significant for invertebrate densities ($p > 0.215$, all pairings; Fig. 3). Both richness ($R^2 = 0.83$) and biomass ($R^2 = 0.83$) were strongly explained by the predictors from the Generalised Linear Models, particularly habitat type, with both metrics also decreasing with increasing distance from the estuary mouth (Suppl. material 1: table S2A). PERMANOVA tests provided strong evidence of habitat differences in the macrofauna community structure ($F = 20.457$, $p = 0.001$), with differences between all habitat combinations ($p = 0.001$, Suppl. material 1: table S3). This is supported by Fig. 4, with distinct clustering of sites by habitat type within the dbRDA plot. These habitat differences in assemblages were strongly correlated to oyster shell (*Magallana gigas*) biomass and pneumatophore densities (Fig. 4). Species most strongly associated with each habitat included isopods (Sphaeromatidae spp.) and little shore crabs (*Brachynotus spinosus*, oyster reefs), Long-legged fly larvae (Dolichopodidae spp., mangroves) and Brazier's hydrococcus (*Hydrococcus brazieri*, bare sediment) based on Dufrene-Legendre analysis (Table 2, Fig. 4).

Remote underwater video nekton assemblages

Remote underwater video (RUV) surveys detected 32 nekton species divided amongst 24 fishes, six decapods and one cephalopod, with a combined abundance (total MaxN) of 3,641 organisms (Fig. 5, Suppl. material 1: table S4A). Nekton were numerically dominated by small pelagic fishes (66.1%), smallmouth hardyhead (*Atherinosoma microstoma*) and blue sprat (*Spratelloides robustus*), followed by King George whiting *Sillaginodes punctatus* (8.3%). Invertebrates comprised 1.4% of abundances and included hermit crabs (*Diogenes senex*), blue swimmer crabs (*Portunus armatus*) and European shore crabs. We observed 29 species from
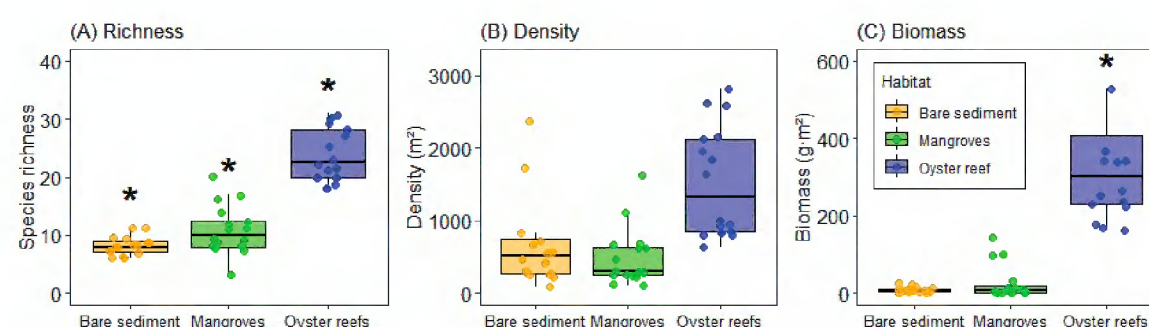

Figure 3. Boxplots showing invertebrate **A** richness **B** density m^{-2} and **C** biomass grams.m^{-2} from excavated quadrat surveys across intertidal habitats (bare sediment, mangrove forests and oyster reefs; n = 48). The boxes represent the 50th percentile (interquartile range), with the median value indicated by a horizontal line within each box. The whiskers extend to the 95th percentile. Overlaid points represent samples. Significant differences between habitats identified from Tukey pairwise comparisons are denoted by asterisk "*".
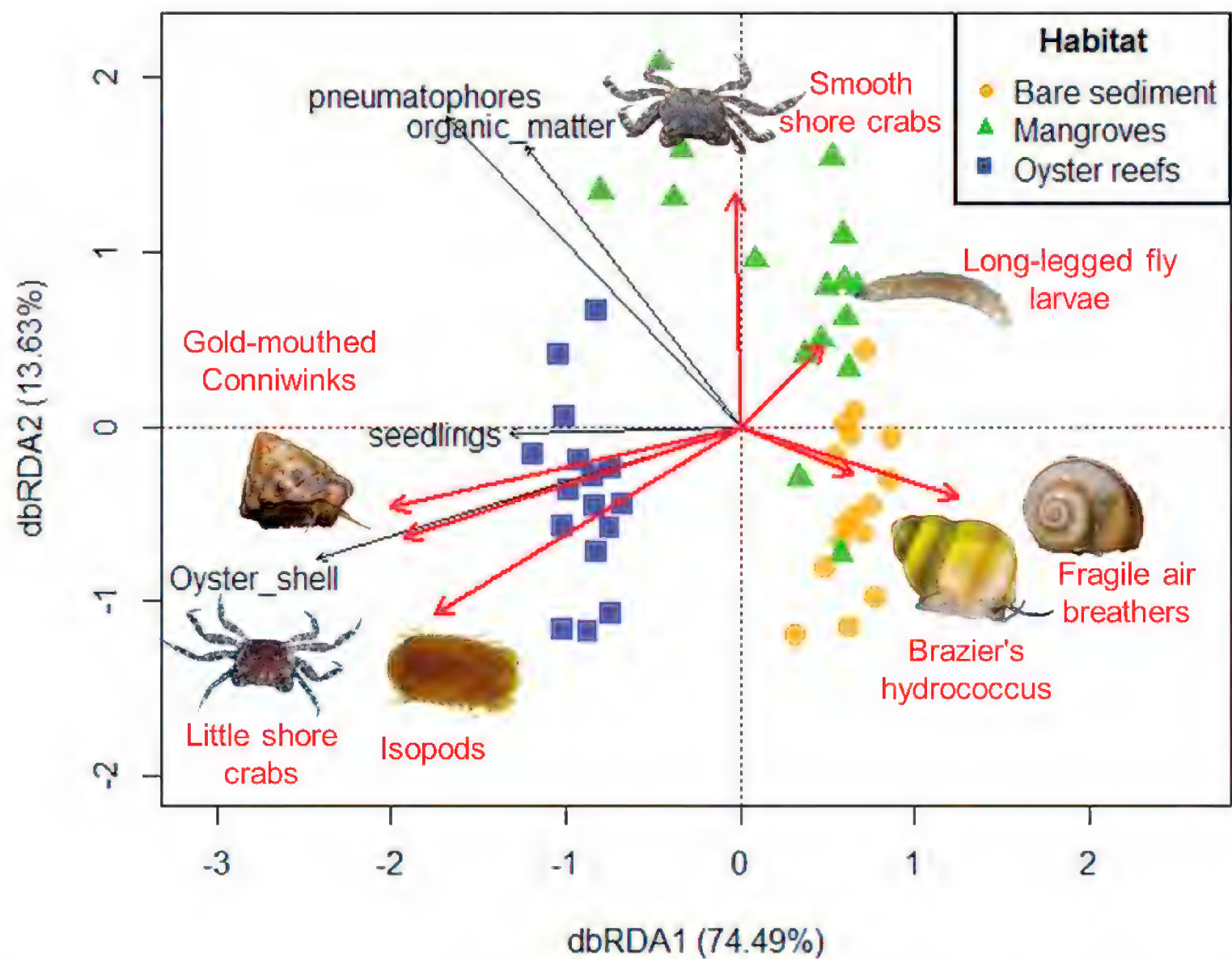
Figure 4. Distance-based redundancy analysis (dbRDA) plots showing the correlation relationships between invertebrate assemblages and environmental predictors associated with the excavated quadrat surveys. Points represent surveys, categorised by habitat. Vectors indicate the direction and strength of significantly correlated ($p < 0.05$) environmental variables (black arrows); and the top indicator species from Dufrene-Legendre indicator analysis (red arrows).

Table 2. Indicator species analysis outcomes, showing the top (≤ 3) species with significant indicator values (IndVal) and their associated p-values for different habitat types. *No indicator species were identified from fyke-net samples.

Species	Habitat	IndVal	p-value
Excavated quadrat surveys			
Isopods Sphaeromatidae spp.	Oyster reef	0.97	0.001
Little shore crabs *Brachynotus spinosus*	Oyster reef	0.97	0.001
Gold-mouthed conniwinks *Bembicium auratum*	Oyster reef	0.93	0.001
Long-legged fly larvae Dolichopodidae spp.	Mangroves	0.49	0.018
Burrowing shore crab *Leptograpsodes octodentatus*	Mangroves	0.25	0.022
Brazier's hydrococcus *Hydrococcus brazieri*	Bare sediment	0.67	0.023
Fragile air breather *Salinator fragilis*	Bare sediment	0.62	0.001
Remote underwater video system surveys			
Oyster blenny *Omobranchus anolius*	Oyster reef	0.66	0.001
Western striped grunter *Pelates octolineatus*	Oyster reef	0.55	0.007
Black bream *Acanthopagrus butcheri*	Oyster reef	0.48	0.046
Yellowfin whiting *Sillago schomburgkii*	Bare sediment	0.59	0.001
Yelloweye mullet *Aldrichetta forsteri*	Bare sediment	0.48	0.039
Smooth toadfish *Tetractenos glaber*	Bare sediment	0.45	0.008

oyster reefs, including 11 that were unique to this habitat, as compared to bare sediment (2 species) and mangroves (1 species). Southern longfin gobies (*Favonigobius lateralis*), black bream (*Acanthopagrus butcheri*) and King George Whiting were the most ubiquitous species observed, occurring in > 75% of video surveys.
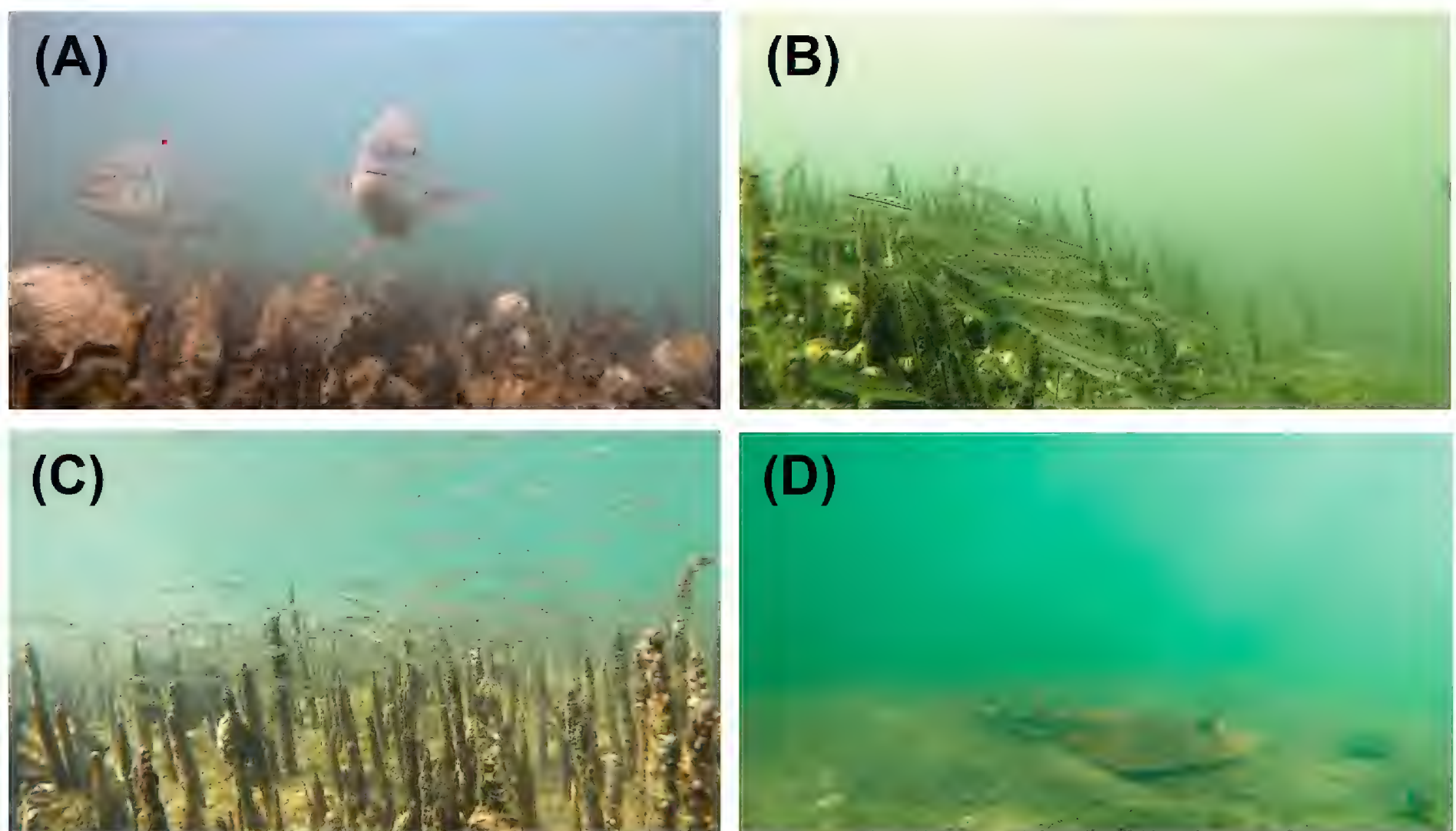
Figure 5. Examples of nekton observed from the remote underwater video (RUV) surveys, including **A** black bream *Acanthopagrus butcheri* **B** juvenile King George whiting *Sillaginodes punctatus* **C** smallmouth hardyheads *Atherinosoma microstoma* and **D** southern fiddler ray *Trygonorrhina dumerilii*.

We observed cryptogenic and/or non-native European shore crabs (n = 4), crested oystergobies (*Cryptocentroides gobioides*, n = 10) and largemouth gobies (*Redigobius microstoma*, n = 1) with 80% of their total abundance derived from oyster-reef surveys (Suppl. material 1: table S4A).

Oyster reefs, on average, were associated with comparatively higher nekton species richness (10.6 ± 0.9 species) and abundances (148 ± 40.2 total MaxN), compared to the other habitats (Fig. 6A, B). Generalised Linear modelling and subsequent Post-hoc Tukey's tests provided strong evidence of greater nekton richness from oyster reefs (p ≤ 0.033, both) and similar, but lower nekton richness amongst mangrove and bare sediment habitats (p = 0.893; Suppl. material 1: table S2B). Additionally, the Generalised Linear Models suggested that total abundances decreased over time during the study period, but increased with increasing distance from the estuary mouth (Suppl. material 1: table S2B). PERMANOVA results indicated habitat differences in the multivariate nekton assemblage from the RUV surveys (F = 18.39, p = 0.001; Suppl. material 1: table S3), contrasting assemblages from oyster reefs and mangroves (p = 0.390), from bare sediment habitats (p < 0.021, both). These trends were predominantly driven by indicator species including oyster blennies and western stripped grunters (*Pelates octolineatus*) in oyster reefs and yellowfin whiting (*Sillago schomburgkii*) and yelloweye mullet (*Aldrichetta forsteri*) in bare sediment habitats (Table 2, Fig. 7A). The indicator test did not identify any nekton species that were strongly associated with the mangrove-dominated habitat (Table 2), likely driven by shared occurrence patterns across two or more habitats (Suppl. material 1: table S4A). Assemblage patterns were strongly correlated to trends in the oyster shell biomass, *A. marina* pneumatophore and seedling cover and distance from the estuary mouth (Fig. 7A).
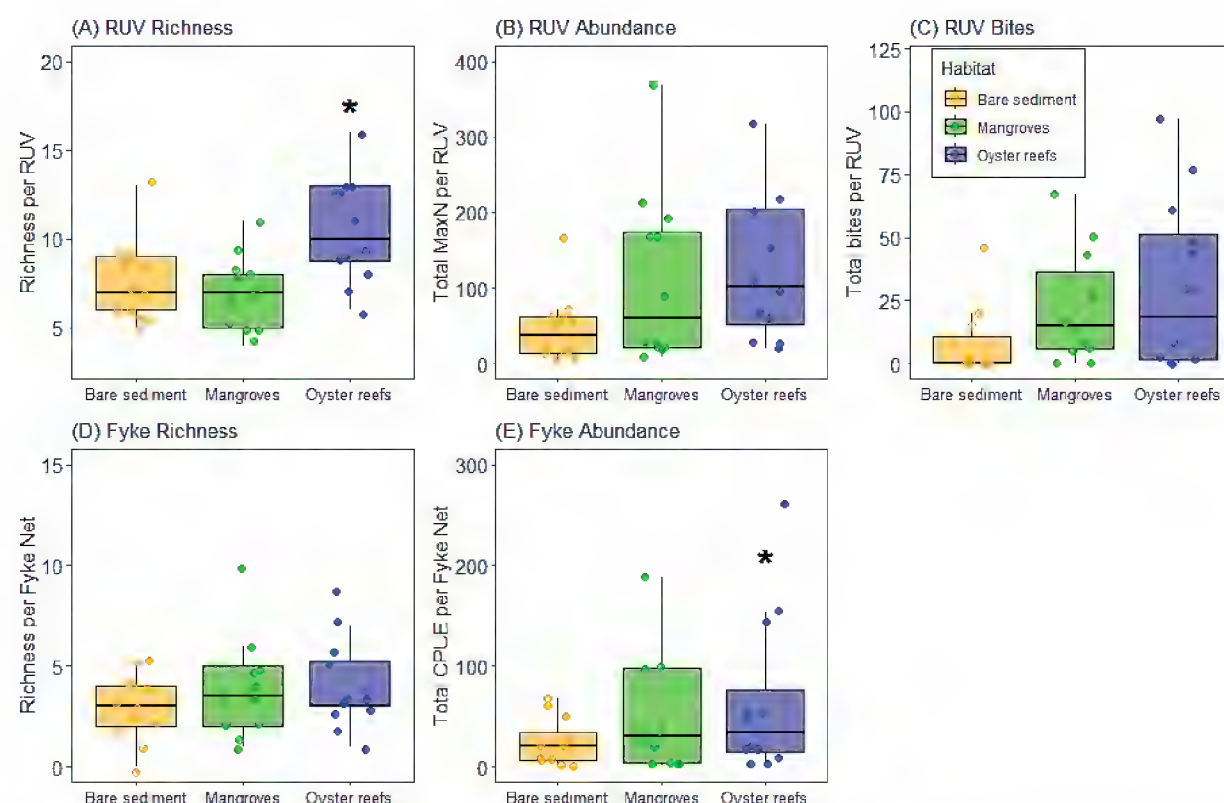
Figure 6. Boxplots showing nekton **A** richness **B** total abundance and **C** bite counts from the remote underwater video (RUV) surveys and **D** richness and **E** total abundance from fyke-net surveys. The boxes represent the 50th percentile (interquartile range), with the median value indicated by a horizontal line within each box. The whiskers extend to the 95th percentile. Overlaid points represent samples. Significant differences between habitats identified from Tukey pairwise comparisons are denoted by asterisk "*".

Fish foraging

Fish foraging behaviour was quantified from 730 bites across 10 different species over the study duration. The most frequent foragers were southern longfin gobies and King George whiting representing 37% and 22% of total observed bites, respectively (Suppl. material 1: table S4A). Most bites were observed in oyster-reef habitats (51%), which, on average, recorded greater bites (30.7 ± 9.9 bites), compared to the mangrove (22.5 ± 6.3) or bare sediment (7.7 ± 4.0) habitats (Fig. 6C). Generalised Linear Models indicated that total bite counts (R^2 = 0.52) were best predicted by habitat type and generally increased with increasing oyster shell and pneumatophore cover, as well as closer proximity to the estuary mouth (Suppl. material 1: table S2B). However, the bite counts were variable across samples, with post-hoc Tukey tests not supporting significant pairwise differences amongst habitats ($p > 0.808$, all pairwise tests; Fig. 6C). Feeding behaviour was exhibited by five fish species at the mangrove and bare sediment habitats each and nine species within the oyster reef habitats.

Fyke-net nekton assemblages

Fyke nets caught 2,195 nektonic organisms representing 19 species divided amongst 14 fish, four decapods and one cephalopod (Suppl. material 1: table S4B). The majority of caught nekton were smallmouth hardyheads (49%), southern longfin gobies (38%) and glassgobies (*Gobiopterus semivestitus*, 5%). Two cryptogenic species, crested oystergobies (n = 2) and exquisite sandgobies (*Favonigobius exquisitus*, n = 1), were also collected, exclusively from oyster reef habitats. Of the caught fish species, 58% were found across multiple habitat types, with the total species richness varying across bare sediment (9 spp.), mangrove (13 spp.) and oyster reefs (15 spp.) habitats.

Generalised Linear modelling found that nekton richness (R^2 = 0.51) obtained from fyke nets increased with closer proximity to the estuary mouth and increasing
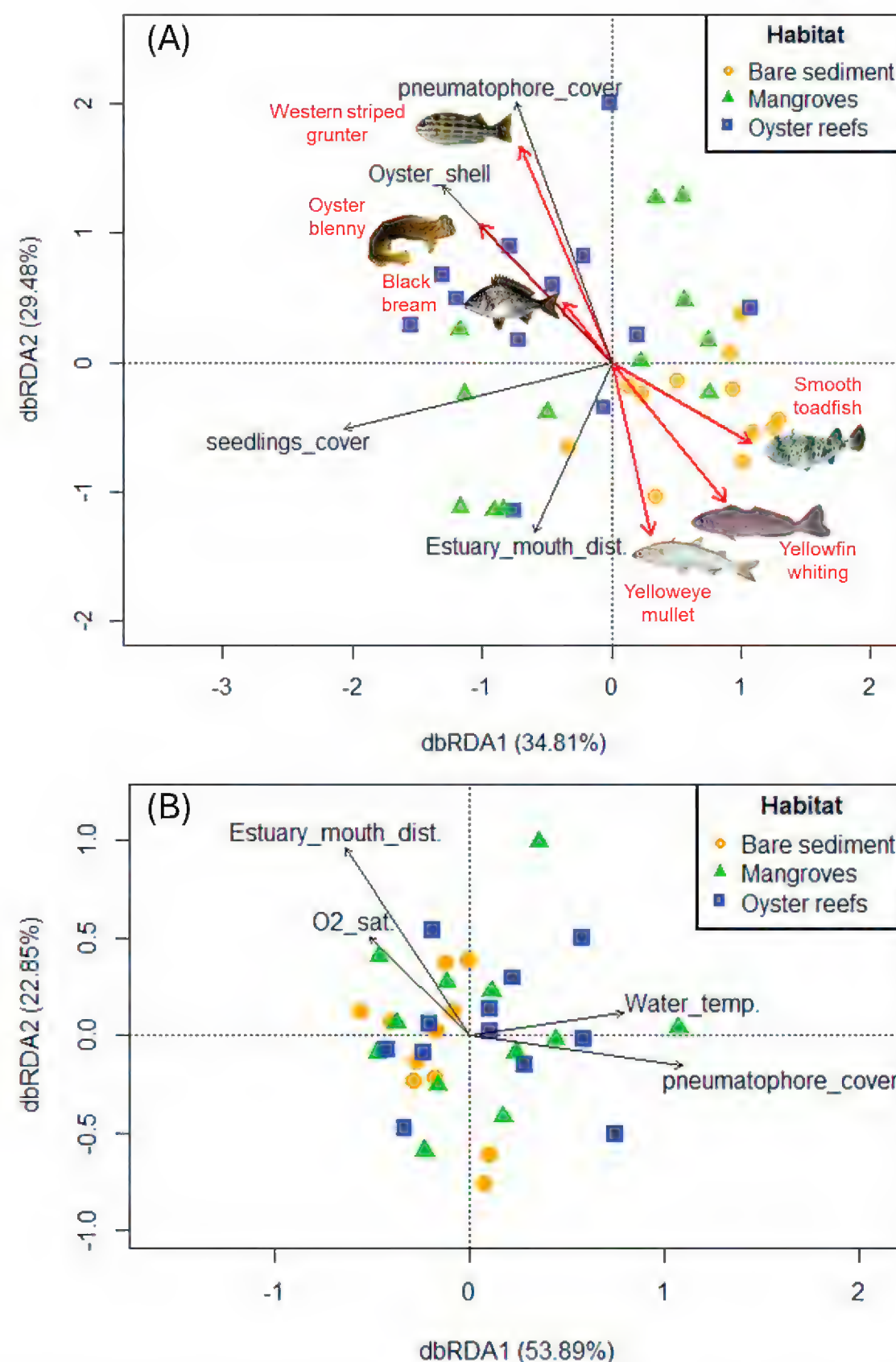
Figure 7. Distance-based redundancy analysis (dbRDA) plots showing the correlation relationships between environmental predictors and the nekton assemblages surveyed using **A** remote underwater video systems (RUV) and **B** fyke nets. Points represent surveys, categorised by habitat. Vectors indicate the direction and strength of significantly correlated (p < 0.05) environmental variables (black arrows); and the top indicator species from Dufrene-Legendre indicator analysis (red arrows).

A. marina seedling cover, with no habitat differences detected (Fig. 6D, Suppl. material 1: table S2C). In comparison, total abundances ($R^2 = 0.55$) was best predicted by habitat type and generally increased with increasing oyster (*Magallana gigas*) shell, with the opposite pattern for *A. marina* seedling cover (Suppl. material 1: table S2C). Post-hoc tests contrasted oyster reef assemblages from the other habitats ($p < 0.002$; Fig. 6E), with average ($\pm$ SE) catches varying across mangroves (92.9 ± 45.5 CPUE), oyster reefs (65.0 ± 23.1 CPUE) and bare sediment (25 ± 6.7 CPUE) habitats. PERMANOVA of the multivariate nekton assemblages from the fyke nets did not support habitat differences (PERMANOVA: $F = 0.720$, $p = 0.775$; Suppl. material 1: table S3), which is reflected by the lack of clustered points in the dbRDA plot (Fig. 7B). While estuary mouth distance and pneumatophore densities were important predictors for the multivariate assemblages (Fig. 7B), we were unable to identify significant indicator species, due to either insufficient sample size or species occurrence across multiple habitats (Table 2).

Nekton length measurements

Length measurements were obtained from 386 individual nekton, from 19 species caught using fyke nets (Table 3). Adult nekton mainly comprised Atherinidae and Gobiidae species, while juveniles included fisheries-targeted King George Whiting (range 72—120 mm total length) and blue swimmer crabs (range 4—25 mm carapace length). Significant habitat differences in size distributions were only identified for southern longfin gobies (χ^2 = 7.34, $p < 0.03$), smallmouth hardyheads (χ^2 = 13.24, $p < 0.002$) and glassgobies (χ^2 = 9.25, $p < 0.01$; Fig. 8). The oyster reefs were associated with larger individuals of each species (average $\pm$ SE: 30.8 $\pm$ 0.9 mm,
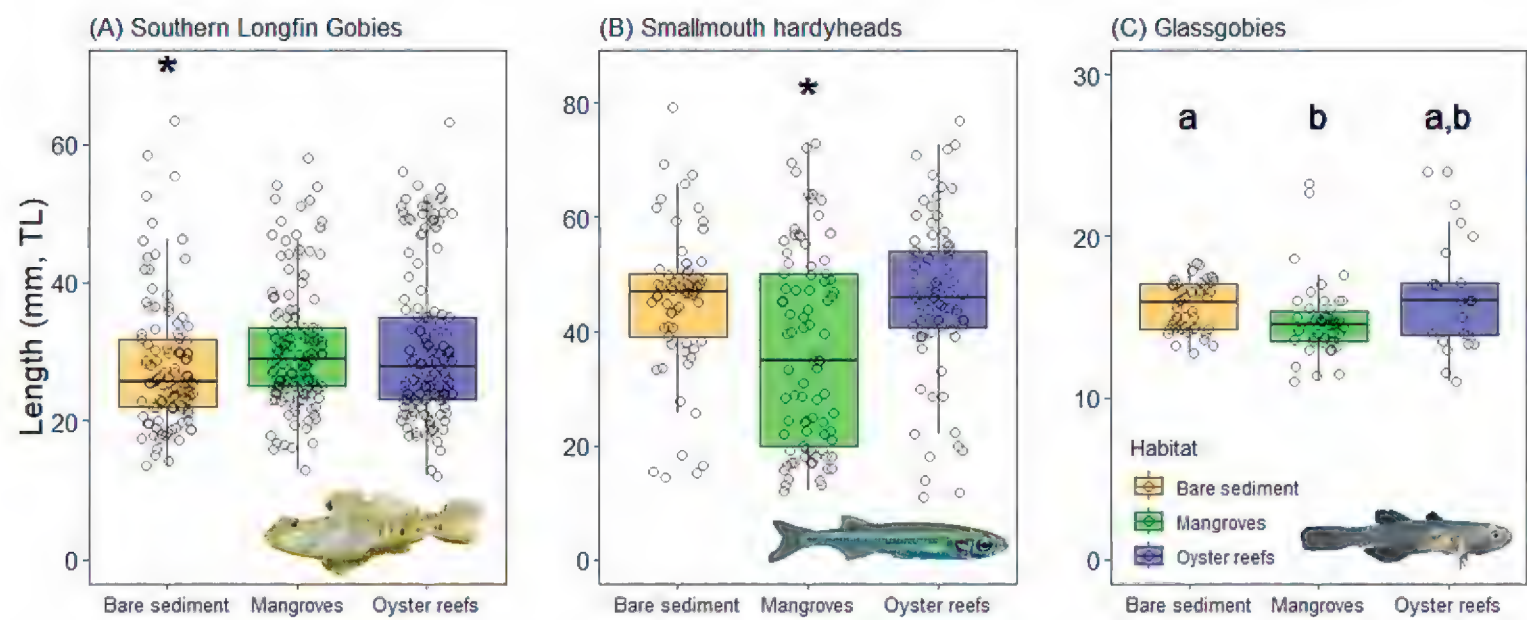

Figure 8. Boxplots of length frequency distribution of total length (mm) for **A** Southern longfin gobies, *Favonigobius lateralis* **B** Smallmouth hardyheads, *Atherinosoma microstoma* and **C** Glassgobies, *Gobiopterus semivestitus*. The boxes represent the 50th percentile (interquartile range), with the median value indicated by a horizontal line within each box. The whiskers extend to the 95th percentile. Overlaid points represent samples. "*" and "a, b" denote results of Dunn's post hoc tests comparing length distributions by habitat type.

Table 3. Total number of individuals per species measured from each habitat (N), body length (millimetres), type (total length (TL), carapace length (CL) or mantle length (ML)) and range (min-max) for each species caught in the fyke nets from Torrens Island.

Species name	Length (mm)	Habitat type					
		Bare sediment		Mangroves		Oyster reefs	
		Total n	Length Range	Total n	Length Range	Total n	Length Range
Acanthopagrus butcheri	TL					1	12.2
Aldrichetta forsteri	TL	6	85.0–120.6				
Atherinosoma microstoma	TL	65	14.4–79.4	85	12.0–73.0	78	11.0–77.0
Bathygobius krefftii	TL			2	42.0–54.0	6	47.2–58.0
Cryptocentroides gobioides	TL					2	32.0–44.0
Diogenes senex	CL	1	4.9–9.4	6	3.6–9.4	9	5.0–10.0
Favonigobius lateralis	TL	107	13.6–63.2	134	13.0–57.9	145	12.0–63.1
Favonigobius exquisitus	TL					1	57
Gobiopterus semivestitus	TL	44	12.8–18.4	46	11.0–23.3	25	11.0–24.0
Kestratherina esox	TL	7	48.0–81.0	5	65.7–84.9	21	43.4–84.8
Neoodax balteatus	TL			1	67.0		
Palaemon intermedius	CL			1	3.0	1	7.0
Pelates octolineatus	TL					1	119.5
Penaeus latisulcatus	CL	1	8.0				
Portunus armatus	CL			10	4.0–19.0	27	6.0–25.5
Pseudaphritis urvillii	TL			1	121.0		
Pseudogobius olorum	TL			5	38.0–55.0	3	24.0–43.0
Sillaginodes punctatus	TL	13	73.9–117.5	6	85.0–120.0	1	72.0
Xipholeptos notoides	ML	2	5.0	1	11.0	7	4.0–11.0

45.2 ± 1.6 mm, 16.4 ± 0.7 mm TL, respectively). On average (± SE), southern longfin gobies were smallest from the bare sediment habitat (28.1 ± 0.9 mm TL), while smaller individuals of the other two species were associated with the mangrove habitat (36.8 ± 1.9 mm, 14.8 ± 0.34 mm, respectively TL) (Fig. 8). For the remaining species, there was insufficient evidence to indicate habitat differences in length measurements, which could be attributed to low sample size or similar length classes present across multiple habitats (Table 3).

Discussion

Despite the ecological risks of non-native habitat-formers globally (Rilov et al. 2024), such as Pacific oysters *Magallana gigas*, our knowledge on the interaction between non-native oyster reefs and invaded ecological systems is poor (Hansen et al. 2023). In contrast, endemic oysters reefs are increasingly associated with valuable ecological functions including habitat provisioning and fish production (Gilby et al. 2018; Connolly et al. 2024), with further enhancements via facilitation cascades with other habitat-formers (Gagnon et al. 2020; Thomsen et al. 2022). We found that, despite its non-native status, 'oyster reefs', formed from the nested co-occurrence of wild Pacific oyster *M. gigas* and grey mangroves *A. marina*, were generally more biodiverse compared to our uninvaded bare sediment or mangrove habitats. These results indicate that non-native oyster reefs may enhance the availability and range of ecological niches and functions, potentially similar to native shellfish reefs.

Pacific oyster habitat characteristics

Within the past decade, non-native Pacific oysters have extensively colonised the Port River-Barker Inlet Estuary. The *M. gigas* population transitioned from sparse individuals (Wiltshire et al. 2010), to dense biogenic oyster reefs, containing an average of 254 alive adults.m^{-2} and 13.2 kg.m^{-2} of oyster material, as identified in our study. These densities exceed those of former endemic oysters (*Ostrea angasi*) which formed reefs at densities of > 50 alive adults.m^{-2} (Gillies et al. 2020). Pacific oyster aggregations modified the habitat characteristics of colonised mangrove forests, establishing complex, biogenic shell matrices. The consolidated surfaces of mangroves can facilitate secondary foundation species, such as epifaunal oysters, by provisioning settlement substrate (Gagnon et al. 2020). Oyster 'reefs' within mangrove forests then arise from successive recruitment and shell accumulation, supported by intraspecific and interspecific facilitation interactions (Reeves et al. 2020) and hydrological influences that aggregate oyster recruits.

Despite high Pacific oyster densities potentially affecting mangroves by limiting gas exchange (Cannicci et al. 2008), similar pneumatophore densities and morphologies were observed in our study, regardless of oyster presence. This could be due to oyster spat initially settling on already mature mangrove root systems, with subsequent settlement preferencing the adult shells of established oyster reefs (Bishop et al. 2012), rather than inhibiting growing pneumatophores. Pacific oysters are, therefore, not substrate limited in this system, based on the presence of extensive pneumatophores and disarticulated cockle shell that were free of oysters. The young age of the reefs (< 10 years) means that negative interactions with established mangroves may not occur until an oyster density threshold is surpassed, which may not manifest for decades (Bazterrica et al. 2022). While the ecological impacts of Pacific

oysters are likely restricted to the fringing shoreline based on tidal inundation patterns, our study provides a baseline suitable for future assessments of these sites to understand long-term variability in species interactions and habitat composition.

Allochthonous material including disarticulated shell material and mangrove debris were found in greater quantities from the oyster reef habitats. Buoyant material, such as mangrove propagules and leaf litter disperse with wave currents and subsequent tidal action (Yun et al. 2022). By modifying the shoreline topography, Pacific oyster shells may trap and retain material, including mangrove propagules (McClenachan et al. 2021) and provide physical protection to newly-settled mangrove recruits (Gagnon et al. 2020). This could explain the high *A. marina* seedling abundances associated with the Pacific oyster reefs. Over longer timeframes, enhanced mangrove recruitment around the *M. gigas* may facilitate mangrove forest expansion, potentially to the detriment of the oysters, as observed in intertidal American oyster *Crassostrea virginica* reefs (McClenachan et al. 2021). While we also hypothesised that oysters may support mangroves through biodeposition, we did not detect habitat differences in soil organic matter in our study. This could be due to: (1) rapid decomposition of material by high macroinvertebrate densities, (2) resuspension and transport of fine organic material during tidal flushing or (3) confounding influences of microbial and microalgae mats across sites (Kristensen et al. 2008). Further investigations are, therefore, needed to understand how *M. gigas* may influence co-existing vegetation and associated fluxes in organic matter.

Habitat value for fish and invertebrates

Oyster reefs in the Port River-Barker Inlet Estuary were mainly found to benefit nekton species that live on or feed near the benthos. Cryptobenthic oyster blennies and Gobiidae species were reef 'residents' within this habitat, consistent with previous studies that have identified their use of disarticulated bivalve shells as nesting sites and refugia throughout the tidal cycle (Hammer 2014; Martinez-Baena et al. 2022). Furthermore, high abundances of fisheries-targeted black bream and western striped grunters could be attributed to foraging behaviour, preferencing the oyster reefs to feed on associated invertebrates, particularly crustaceans and bivalves (Sarre et al. 2000; Potter et al. 2022). While fyke nets were less sensitive to detecting species-specific distribution trends, the larger small-bodied fishes from the oyster reef habitats could indicate size-based habitat preferencing or favourable environmental conditions. Nekton community composition from the RUV surveys was most similar between sites dominated by mangroves, with and without Pacific oyster aggregations. We hypothesise that this was driven by species-specific trends and some functional redundancy between habitats resulting from the shared co-occurrence of *A. marina* structures like pneumatophores. For example, small pelagic fishes (e.g. Atheriniformes) were common to both habitats and may access fringing mangroves for refugia at high tide (Henkens et al. 2022). Given that we observed foraging behaviour across habitat types, assessments such as stomach contents, predation assays or stable isotope analysis, could be valuable for understanding trophic linkages of these habitats and associated species (Martinez-Baena et al. 2023; Martin et al. 2024), including.

During our study, seven non-native and/or cryptogenic species were sampled exclusively or in greater numbers from the oyster reefs, including the first confirmed specimens of the Hercules club whelk (*Pyrazus ebeninus*) and exquisite

sandgoby (*Favonigobius exquisitus*) in South Australia. Thus, Pacific oyster aggregations may facilitate secondary invasions by other non-native species by creating favourable habitat conditions (Reise et al. 2023). For example, the European shore crab (*Carcinus maenas*) and crested oystergoby (*Cryptocentroides gobioides*) from eastern Australia are strongly associated with intertidal shellfish ecosystems in their respective native ranges (Troost 2010; Martinez-Baena et al. 2022). These species, therefore, should respond positively when introduced into similar environmental conditions (O'Loughlin and Green 2017). The presence of non-native species alongside native counterparts at our study site could result in inter-specific competition of shared resources and direct predation (Hammer 2014; Gallardo et al. 2016). Of particular concern are *C. maenas*, which may indirectly facilitate Pacific oysters by consuming their competitors. They exhibit dietary preferences for mussels over oysters (Joyce et al. 2020), posing a threat to the native *Brachidontes* and *Xenostrobus* mussels found at our sites (Campbell et al. 2019).

Our combination of excavated quadrat, RUV and fyke-net surveys in dynamic intertidal habitats provided comprehensive information about estuarine fish and invertebrate habitat distributions across multiple spatial-scales (Stein et al. 2014). Fine-scale variation in benthic structure was found to strongly influence invertebrates and, while we did not detect consistently high total invertebrate densities in oyster reefs (Grabowski et al. 2005), our results suggest that these habitats support enhanced invertebrate species richness and biomass and, therefore, potentially offer diversified foraging resources (Martinez-Baena et al. 2023). These results conform to previous assessments of oyster reef associated invertebrates (Bishop et al. 2012; McAfee et al. 2016), which may benefit from enhanced shelter, settlement surfaces and trophic resources.

Both RUV and fyke nets have been applied in intertidal shellfish ecosystems elsewhere in the world (reviewed in Martin et al. (2024)) and offer complimentary information when used in combination (Orfanidis et al. 2021). Specifically, unbaited RUV surveys target large-bodied species and record natural behaviour, while fyke nets enhance surveys and measurements of small-bodied nekton (e.g. Orfanidis et al. (2021); Martinez-Baena et al. (2022)). Similarly, by sampling both the outgoing tide (i.e. RUV and fyke nets) and at low tide using extractive quadrats, it is possible to infer the tidal movement of different species and identify resident species that are strongly associated with habitats throughout the tidal cycle. This approach is particularly relevant for intertidal ecosystems as transient species vary their habitat use, based on tidal accessibility and resources availability (Grabowski et al. 2005; Martin et al. 2024). For example, nekton metrics in our study were highly variable within habitats and over the study period, suggesting that broader spatio-temporal influences, such as environmental gradients or seascape composition, could be impacting species distributions and behaviour across habitats (e.g. Jones et al. (1996); Perry et al. (2023)). This is further supported by distance from the estuary mouth being an important predictor for fish and invertebrate metrics, which may have confounded habitat patterns across sites. We recommend that practitioners assessing intertidal oyster reefs incorporate multiple sampling methods to effectively monitoring biodiverse assemblages and to consider different environmental variables that may influence or limit different approaches.

In contrast to other non-native species, invasions by bivalves generally facilitate enhanced biodiversity through positive ecological interactions, such as increasing habitat complexity and ameliorating stresses (Guy-Haim et al. 2018). Oyster reefs are known to benefit fish and invertebrate communities by provisioning high value

foraging and nursery habitat and reducing abiotic and biotic stressors (e.g. predation, desiccation; Reeves et al. (2020); zu Ermgassen et al. (2021)). Our results concur with recent studies that have reported positive oyster reefs interactions with fish and invertebrate communities in mangrove-dominated systems (e.g. Gilby et al. (2019); Martinez-Baena et al. (2022); Perry et al. (2023)). For example, Perry et al. (2023) found that the fish species richness and harvestable fish abundance in structured habitats positively responded to oyster cover. Similarly, McAfee et al. (2016) showed that oyster aggregations in mangrove forests facilitated elevated invertebrate richness and abundances, compared to mangroves without oysters. These results can be attributed to facilitation cascades and other positive interactions resulting from the combination of mangroves and oysters, which synergistically enhance the diversity and availability of niches and resources (Stein et al. 2014; Thomsen et al. 2022).

Management implications of non-native oyster reefs

Our findings indicated that non-native oyster reefs are influencing species and assemblage structure, but generally had beneficial impacts such as enhanced biodiversity and positive associations with fisheries-targeted species. While not quantified, these reefs may support other valuable socioecological outcomes including nutrient sequestration, enhanced water visibility and human shellfish harvesting (McAfee and Connell 2021; Hansen et al. 2023). Subsequently, in regions were *M. gigas* are naturalised, such as northern Europe, the oysters have supported the development of new 'gastro-tourism' opportunities (Mortensen et al. 2019) and have been adopted in shoreline stabilisation structures (Walles et al. 2016). This has been partially supported by the functional similarities of *M. gigas* to diminished native bivalves and subsequent recovery of lost ecological functions (Zwerschke et al. 2019; McAfee and Connell 2021). As highlighted by Howie and Bishop (2021), non-native oysters may be considered for the restoration of ecological services, particularly in naturalised regions where analogous native species have failed to recover or adapt to modified environmental conditions. However, *M. gigas* may only partially restore functions of lost subtidal shellfish reefs (e.g. *O. angasi* in South Australia) and potentially establish novel, yet beneficial conditions in regions that historically lacked comparable habitats (Guy-Haim et al. 2018; McAfee and Connell 2021). In an anthropogenically changing world, the positive benefits of non-native habitat formers must increasingly be studied and considered to conserve and enhance ecological services (Rilov et al. 2024).

The capacity of non-native habitat-formers to modify ecological services and community composition poses a management challenge for scientists and policy-makers (Rilov et al. 2024). Beyond the risk of secondary invasions, Pacific oysters can induce other socioecological impacts including changes in landscape aesthetics, channel navigation and aquaculture interactions (e.g. disease transmission, genetic exchange; Herbert et al. (2016); Hansen et al. (2023)). Furthermore, positive ecological benefits to endemic species may change through time with increasing *M. gigas* dominance or induce unexpected negative cascades in adjacent habitats. Efforts to mitigate Pacific oysters is further complicated by its dual status as both an aquaculture species and marine pest (Martínez-García et al. 2022). Cultivation of *M. gigas* outside their native range can support non-native reef establishment through repeated seeding and genetic enhancement from aquaculture stock (McAfee and Connell 2021). Furthermore, efforts to completely eradicate and prohibit *M. gigas* aquaculture are unlikely, due to the negative socio-economic

impacts and low likelihood of success (Troost 2010; Hansen et al. 2023). Subsequently, management of non-native oyster reefs needs to be evidence-based with consideration of both favourable and undesirable socioecological outcomes within the local regional context (Martínez-García et al. 2022). For example, *M. gigas* expansion into vulnerable and protected ecosystems could be mitigated by regulating aquaculture permissions and implementing harvesting regimes (Hansen et al. 2023). In anthropogenically modified estuaries, however, we expect that non-native oyster reefs may provide more socioecological benefits compared to potential harm, but these habitats require monitoring, regardless of the mitigation strategy.

Conclusion

Non-native habitat-formers, such as Pacific oysters *Magallana gigas*, can pose a significant socioecological challenge for managing coastal ecosystems. In this study, we evaluated the ecological interactions of non-native *M. gigas* on mangrove forest biodiversity, particularly effects on fish communities. Our findings indicate that, despite their non-native status, *M. gigas* can facilitate positive interactions with grey mangroves, leading to subsequent enhancements in fish and invertebrate diversity, prey availability and foraging opportunities. We also identified that oyster reefs supported fisheries-targeted species and may facilitate habitat conditions favourable to a greater range of species and functions. However, oyster reefs facilitated both native and non-native species, including previously undocumented species. Thus, we describe potential ecological outcomes of non-native habitat-formers and outcomes from the global expansion of non-native Pacific oyster reefs in vegetated coastal estuaries.

Acknowledgements

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

This study was conducted following the ethical standards of Flinders University and relevant national and international laws. Necessary permits were obtained, including animal ethics approvals from Flinders University (5635 & 5642), a scientific research permit from the SA Department of Environment and Water (DEW) (M27219-1), and a Ministerial permit from The Department of Primary Industries and Regions, South Australia (PIRSA) (ME9903230).

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Author contributions

Bradley Martin, Ryan Baring, Charlie Huveneers and Simon Reeves conceptualised the idea and methods for this study. Bradley Martin led the fieldwork, sample processing and initial data analysis. Bradley Martin led the writing and created the figures and Ryan Baring, Charlie Huveneers and Simon Reeves provided crucial contributions to the manuscript. Ryan Baring, Charlie Huveneers and Simon Reeves supervised the project. All authors give their approval for the publication of this manuscript in its final support.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary figures and tables

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Data type: docx

Explanation note: **figure S1.** Collinearity matrices for environmental predictors related to ecological patterns. **figure S2.** Boxplot of length frequency distribution of grey mangrove (*Avicennia marina*). **figure S3.** Frequency histogram. **table S1.** List of macrofauna species obtained from the extractive quadrats. **table S2.** Results of generalised linear models. **table S3. A** PERMANOVA and post-hoc pairwise outputs. **table S4.** List of nekton species identified.

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